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THE STRUCTURE OF THE MAPLE-BEECH ASSOCIATION IN NORTHERN MICHIGAN

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THE STRUCTURE OF THE MAPLE–BEECH ASSOCIATION IN NORTHERN MICHIGAN

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INTRODUCTION

The northern part of the Lower Peninsula of Michigan was originally occupied chiefly by two plant associations, the one characterized by Norway pine and white pine, and the other by sugar maple and beech. Only a small proportion of the area was held by the numerous minor associations which constitute the varied vegetation of bogs, swamps, shores, and dunes. Of these two important associations, the pine forest was composed chiefly of northern species, which in this region were near or at their southern limit, while the hardwood forest of beech, elm, basswood, sugar maple, and other deciduous trees included chiefly southern species, which found their northern limit of distribution here or a comparatively short distance farther north.

Abundant evidence has been brought forward to show that the pine forests are a part of a great series of associations which have been closely related to one another since pre-glacial time, which are connected by certain definite successional trends, and which occupy the same general range, extending in a broad belt across the continent from Alaska to Newfoundland. The hardwood forest is, similarly, a part of another great vegetation-complex, occupying most of the land between the Missouri Valley and the Atlantic Ocean and between the Great Lakes and the southern end of the Appalachian Mountain system. It has also been shown for this portion of Michigan, and the same condition is doubtless true for many other regions as well, that there is great competition between the various associations of these two complexes wherever they come in contact, and that

in general the associations of the southern complex tend to displace those of the northern. This was early demonstrated by Whitford (1901) and needs no further discussion here. Again, it seems entirely probable that this present tendency is only the continuation of a similar competition between the two types of vegetation which has existed since shortly after the close of the last glacial period, the general result of which (Gleason, 1923) has been the retreat northward of the pine forests and the associations related to them for some three hundred or four hundred miles and the corresponding advance of the hardwood forest for the same distance.

Numerous papers have appeared during the past two decades dealing with the general ecology and distribution of these two types of vegetation. Two of the more recent are those by Clayberg (1920), who well describes the environment and the life-history of the maple-beech forest and its relations to the other associations of the region, and by Quick (1924), who discusses the general distribution of the association throughout the Lower Peninsula of Michigan. Both authors cite the important earlier papers in their bibliographies.

No paper, however, has so far presented a full statement of the floristic structure of this exceedingly important association. Since it is rapidly disappearing before the encroachment of the lumberman, it seems highly desirable to put on record an account of the component species and of their relative importance. During the summer of 1923, the writer accompanied Dr. Lee R. Dice, of the Zoölogical Museum of the University of Michigan, on a reconnaissance of some large tracts of virgin maple-beech forest, and to the observations made then he has added others made by him at various times and places in the same general region.

AREAS EXAMINED

1. A square mile of virgin forest on Section 13, Town 30 North, Range 5 West, in the extreme eastern end of Antrim County, bordering on Otsego County, about six miles east of

Alba. The whole surface is essentially flat and without surface drainage; soil sandy, allowing easy percolation of rain water; altitude about 1200 feet.

2. A square mile on Section 8, Town 30 North, Range 4 West, near the western end of Otsego County, about two miles northeast of Area 1 and with the same topography and soil.

3. A square mile on Section 17, Town 30 North, Range 4 West, in Otsego County, adjoining Area 2 on the south and with the same topography and soil.

4. A tract almost a square mile in extent on Section 35, Town 32 North, Range 4 West, in the eastern end of Charlevoix County, about eight miles north of Area 2. The surface is rolling, freely traversed by narrow ravines with gently sloping sides which carry flood waters only; soil sandy; altitude probably about 1000 feet and distinctly lower than the high morainic hills of the vicinity.

5. A small tract, not exceeding forty acres in extent, on the land of the State Game Refuge in Emmet County, about nine miles southwest of Mackinaw City, on an old beach of Lake Nipissing; soil sandy; surface level; altitude about 650 feet. The area is completely surrounded by coniferous forest, composed chiefly of arbor-vitae and balsam on the low ground of the same general level and of pine on the adjoining high fossil dunes.

METHOD

The composition of the dominant forest layer was determined by counting all the trees six inches or more in diameter on a strip about fifty feet wide extending across the area, and the results are here expressed in percentages. The frequency of the secondary species, including the herbs, shrubs, and seedling trees, was determined by listing every species in each of 100 quadrats one meter square. The results of this count are expressed by a percentage known as the frequency index, showing the percentage of the total quadrats examined (in this case 100 in each area) in which the species actually occurs. The quadrats were located in a strip, spaced ten paces apart, and the strip

is accordingly 1000 paces long, extending across the area, or back and forth in the small Area 5. Quadrats were in every case counted where they lay, no matter what might be the local conditions on each. Thus some were largely occupied by large trees, others by fallen logs, and others by dense thickets of shrubbery. Determination of the frequency index by this method is of course impartial: it indicates the important species, expresses the relative importance and commonness of each, and gives a basis of data upon which the total number of species may be calculated with a high degree of accuracy. In addition to these statistical observations, all other species of vascular plants were listed so far as noted.

In every plant association of considerable age and general uniformity of environment, of which the maple-beech forest is an excellent illustration, the vegetation attains also a great uniformity. A hundred quadrats, scattered widely over an area, are sure to include all the typical species and the frequency index shows their relative importance. Other species of minor importance may be represented by so few individuals that they are not included in any of the quadrats, but are noted elsewhere, while still others may escape attention completely unless every square foot of the area is searched. The number of these unobserved species may be estimated with great accuracy, since the increase in number of species from small tracts to large varies as the logarithm of the area.

In the following tables, the frequency index of each species is expressed in figures, the presence of a species outside the quadrats is indicated by x, and blanks indicate that the species was not observed in the area. The first table refers only to trees more than six inches in diameter, while reference to trees in the second table pertains only to seedlings and saplings. Scientific names follow the usage of Gray's *New Manual of Botany*, with the exception of certain species of Carex, for the identification of which the writer is under obligations to Mrs. John H. Ehlers.

TABLE I

COMPOSITION OF THE FOREST COVER

SPECIES	AREA			
	1	2	3	4
Acer Saccharum	91	75	75	48
Betula lutea	4	1	4	x
Fagus grandifolia	x	1	5	28
Ostrya virginiana	..	x	1	..
Tilia americana	1	4	1	1
Tsuga canadensis	x	1	5	3
Ulmus americana	4	18	9	20

TABLE II

FREQUENCY INDEX OF SECONDARY SPECIES

A. SPECIES NORMALLY ASSOCIATED WITH THE MAPLE-BEECH ASSOCIATION

SPECIES	AREA				
	1	2	3	4	5
Acer Saccharum	100	100	100	100	100
Acer spicatum	3	9	5	10	..
Actaea alba	x	x	..	..	3
Adiantum pedatum	1	4	x	9	..
Aralia nudicaulis	20	36	45	24	4
Aralia racemosa	x	..	x	1	..
Arisaema triphyllum	x	8	x	13	..
Asarum canadense	..	..	..	1	..
Aspidium spinulosum	44	41	67	38	..
Betula lutea	3	x	x	1	3
Botrychium virginianum	1	..	..	..	x
Brachyelytrum erectum	x	..	1	..	..
Carex arctata	1	..	4	3	..
Carex convoluta	..	..	..	x	..
Carex intumescens	4	3	1	x	..
Carex laxiflora latifolia	..	..	..	x	..
Carex leptonervia	..	..	1	..	2

TABLE II — *Continued*

FREQUENCY INDEX OF SECONDARY SPECIES

A. SPECIES NORMALLY ASSOCIATED WITH THE MAPLE-BEECH ASSOCIATION

SPECIES	AREA				
	1	2	3	4	5
Caulophyllum thalictroides	x	x	x	x	..
Cornus alternifolia	1	1	x	x	..
Corylus rostrata	..	x	1	..	..
Cystopteris fragilis	..	..	1	x	x
Fagus grandifolia	x	2	5	70	14
Fraxinus americana	..	..	..	3	..
Galium triflorum	11	22	7	20	x
Geranium Robertianum	..	7	x	2	..
Hepatica acutiloba	..	..	..	2	..
Melica Smithii	..	1	x	5	..
Milium effusum	3	8	11	3	..
Mitella diphylla	..	..	..	x	..
Monotropa uniflora	..	..	..	..	1
Osmorhiza Claytoni	10	51	3	78	1
Ostrya virginiana	..	x	x	x	..
Oxalis Acetosella	..	..	x	..	..
Polygonatum biflorum	18	8	10	8	..
Psedera quinquefolia	..	..	..	3	..
Ribes Cynosbati	4	8	2	1	..
Sambucus racemosa	9	32	9	23	..
Smilacina racemosa	x	2	2	5	13
Streptopus roseus	3	x	6	..	..
Thalictrum dioicum	x	..	..	..	..
Tiarella cordifolia	59	50	40	20	..
Tilia americana	2	3	1	2	..
Trillium grandiflorum	3	x	5	7	3
Ulmus americana	22	21	23	18	..
Ulmus fulva	x	..	..	..	..
Viburnum acerifolium	1	x	..	..	..
Viola scabriuscula	28	59	13	41	..

TABLE II — *Continued*

B. SPECIES NORMALLY ASSOCIATED WITH CONIFEROUS FORESTS, EITHER OF BOG OR OF UPLAND

SPECIES	AREA				
	1	2	3	4	5
Abies balsamea	..	..	..	..	x
Aster macrophyllus	..	..	1	..	x
Circaea intermedia	..	1	..	1	..
Clintonia borealis	..	..	x	..	1
Cornus canadensis	..	..	..	..	x
Lonicera canadensis	1	1	4	x	4
Lycopodium annotinum	..	..	..	..	12
Maianthemum canadense	2	3	14	5	13
Mitchella repens	2	3	5	5	35
Pinus Strobus	..	..	x	..	..
Pyrola americana	..	..	..	..	x
Pyrola secunda	..	..	..	..	4
Streptopus amplexifolius	x	..	..	..	..
Taxus canadensis	x	6	2	x	25
Trientalis americana	2	..	4	..	41
Trillium cernuum	x	..	..	..	..

C. SPECIES NORMALLY ASSOCIATED WITH THE ASPEN FOREST

SPECIES	AREA				
	1	2	3	4	5
Acer pennsylvanicum	..	..	..	x	14
Acer rubrum	x	..	..	..	..
Diervilla Lonicera	..	..	1	.	..
Hamamelis virginiana	..	..	x	..	..
Lactuca spicata	x	x	..	x	..
Oryzopsis asperifolia	..	..	x	..	..
Polygonum cilinode	..	x	..	..	..
Prunus virginiana	1	..	x	x	x
Rubus allegheniensis	4	2	21	..	..
Rubus idaeus aculeatissimus	..	16	..	..	..

TABLE II — *Concluded*

D. MISCELLANEOUS OR UNIDENTIFIED SPECIES

SPECIES	AREA				
	1	2	3	4	5
Asplenium filix-femina	..	..	..	..	x
Carex sp	..	..	..	..	x
Corallorhiza sp	..	..	..	..	x
Prunus serotina	x	x	2	..	..
Viola sp	10	9	1	..	x

GENERAL DISCUSSION

A survey of the preceding tables reveals some interesting conditions and enables us to draw certain conclusions respecting the ecology of this association. A summary of the statistical matter may first be presented. The total number of species observed is 79, of which 78 occur as secondary species in the ground cover, and 7 are trees which at maturity form the forest cover. Other species of trees are represented, of which mature individuals were not observed. Hemlock is the single arborescent species of which young plants were not detected.

The average number of secondary species per meter quadrat is 2.93 in Area 5, and varies from 3.73 to 5.17 in Areas 1 to 4. The probable total number of species for a square mile of the association is computed to range from 84 in Area 1 to 100 in Area 3, and the total flora of the association in the northern part of the Lower Peninsula probably does not exceed 200 species, excluding those recently introduced as a result of grazing, partial clearing, occasional fires, or other human activities.

The allotment of species among the four ecological groups may be open to criticism. As they stand, however, the first, containing the species considered to be normal to the maple-beech association, includes 23 species represented in four or all of the five areas, and 24 species limited to three areas or fewer. Groups B and C, containing the casual species, include only five

of general distribution through four or all of the areas, and 21 restricted to three areas or fewer, and two-thirds of these are reported from a single area only. The average frequency index of the species in Group A is 13; Group B, 5; Group C, 3; Group D, 2. Within Group A, those species which are represented in four or five areas have an average frequency of 18, which sinks to 1 for the species limited to three or fewer areas.

Twenty-three species are accordingly indicated by the tables as the characteristic species of the association, distinguished not only by wide distribution among the areas, but also by high frequency indexes within the areas. These species are as follows:

TREES

Acer Saccharum	Tilia americana
Betula lutea	Ulmus americana
Fagus grandifolia	

SHRUBS

Acer spicatum	Ribes Cynosbati
Cornus alternifolia	Sambucus racemosa

HERBS

Adiantum pedatum	Milium effusum
Aralia nudicaulis	Osmorhiza Claytoni
Arisaema triphyllum	Polygonatum biflorum
Aspidium spinulosum	Smilacina racemosa
Carex intumescens	Tiarella cordifolia
Caulophyllum thalictroides	Trillium grandiflorum
Galium triflorum	Viola scabriuscula

It is probable that other prevernal species belong in this category, but these plants had completed their vegetative cycle and disappeared above ground before August, when this survey was made.

A high frequency index necessarily requires a large number of individuals, and it is generally true that the number of individuals of any species is an indication of the degree of its adaptıon to the environment. These twenty-three species are accordingly distinguished, in general, as the ones best fitted to live and multiply in the prevailing environment and under the strenuous competition of the maple-beech forest. Some of them have a uniformly high frequency index, as *Acer Saccharum*, *Aspidium spinulosum*,

and *Tiarella cordifolia*; others are very constant in their abundance, as *Ulmus americana*, but a few show striking variations in frequency, as *Osmorhiza Claytoni* and *Fagus grandifolia*. In the latter cases, the variation is too great to be ascribed merely to chance, and a causal difference in environment is suggested. The nature of these environmental differences, if they exist, cannot be accurately determined except by experimental methods, but there is good reason, in the case of *Fagus grandifolia* at least, for believing that soil moisture is the controlling factor.

In Areas 1, 2, and 3 the terrain is high and level. Rain-water percolates into the ground at once and doubtless reaches a considerable depth, later to emerge in springs around the margin of the plateau on which these areas are situated. In these three areas beech is relatively rare, especially in the seedling stage. But in Area 4, situated on rolling ground at a lower elevation and probably better supplied by water by seepage, seedling beech is abundant and mature trees constitute a considerable part of the forest. In a tract of hardwoods on the northwest shore of Burt Lake, where subterranean water seeps out into several boggy spots, mature beeches constitute 42 per cent of the forest, and the frequency index of seedlings rises to 43. Along a bluff west of Douglas Lake, now cleared, beech originally composed 28 per cent of the forest cover. During the dry summer of 1923, it was very evident that beech seedlings were suffering from drought in the first three areas, while in Area 4 they showed no sign of such injury. It is probably safe to conclude that the proportion of beech in the association depends chiefly on the amount of available water.

Hemlock is present in all five areas in a small and rather variable amount, but hemlock seedlings were not observed. Records by Dr. Frank C. Gates or by the writer, extending over a period of thirteen years at the Biological Station of the University of Michigan in Cheboygan County, indicate that reproduction of hemlock is very rare, and the general deficiency of hemlock saplings shows that this condition has prevailed for many years. Almost all hemlock trees in the hardwood forests of the region are veterans. After their death, which may be

expected in a comparatively short time, hemlock will practically disappear as a component of the association. On the other hand, conditions were undoubtedly favorable for the establishment of hemlock some three centuries ago, when the present veterans were seedlings. Such a period is too short to expect any fundamental climatic variation to have taken place, and it is more plausible to assume tentatively that the chief environmental change has been caused by the vegetation itself. The forest cover has a great effect on the environment of the ground vegetation, through its control of light, through its effect on the physical nature of the soil by the addition of fallen vegetable matter and the chemical nature by the decomposition of twigs and leaves, and through its control of the soil fauna and flora. Whatever the vegetation of three hundred years ago may have been, it evidently produced an environment in which hemlock seeds could germinate and grow, and that is not true of the present forest cover of maple and beech.

If the general successional relations of the coniferous and deciduous forests, as described by Whitford, are conceded, it follows that, in general, the youngest part of the deciduous forest is near its margin where it comes in contact with the earlier coniferous associations, and that small detached bodies of hardwood are generally younger than those of large extent. Areas 1 to 3 are all parts of a great body of maple-beech forest which originally covered many square miles of land without interruption, while Area 5 is a small detached body, several miles from the nearest forest of the same type. In Area 2 for example, there are 30 species assigned to Group A, species characteristic of the hardwood association, with an average frequency index of 16, and only five species of Group B, including those normal to coniferous forests, with an average frequency index of 3. In Area 5, Group A is represented by only 13 species, with an average frequency of 11, while Group B has 12 species with an average frequency of 11. The contrast between the two areas, as shown by these figures, is striking, and may well indicate that Area 2 is considerably older than Area 5, either ecologically or chronologically, and perhaps both.

There is other ecological evidence, largely of a circumstantial nature, pointing to the same conclusion, which may be expressed by the following general theory: The hemlock forest represents the mesophytic climax of various successional series of the northern type of vegetation, and the veteran hemlocks of the modern hardwood forest are the last generation of trees of this earlier association. Succession by hardwood forests is a modern process, which in some places has not yet been completed in respect to the secondary species, and the present veteran trees of sugar maple and beech represent, in some places at least, the first generation of dominant species of this association.

GENERAL CONCLUSIONS

1. The hardwood forest of the region is dominated by sugar maple, with beech, birch, elm, and basswood as important co-dominants, the proportions of each depending on the available moisture.

2. The flora of the association includes some two hundred species of vascular plants, of which about a score are regarded as characteristic, and of which many others are chance invaders from neighboring associations or relicts of an earlier occupation of the land by coniferous forest. Hemlock belongs in the latter category.

3. The hardwood forest is still young historically and may have attained its full ecological dominance only one generation (about three centuries) ago.

New York Botanical Garden

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